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## Inconsistency Between Socio-Spatial and Genetic Structure in a Coastal Dolphin Population

Chabanne, Delphine B H ; Allen, Simon J ; Sherwin, William Bruce ; Finn, Hugh ; Krützen, Michael

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# Inconsistency Between Socio-Spatial and Genetic Structure in a Coastal Dolphin Population

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Identifying population structure and boundaries among communities of wildlife exposed to anthropogenic threats is key to successful conservation management. Previous studies on the demography, social and spatial structure of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) suggested four nearly discrete behavioral communities in Perth metropolitan waters, Western Australia. We investigated the genetic structure of these four communities using highly polymorphic microsatellite markers and part of the hypervariable segment of the mitochondrial control region. Overall, there was no evidence of spatial genetic structure. We found significant, yet very small genetic differentiation between some communities, most likely due to the presence of highly related individuals within these communities. Our findings of high levels of contemporary migration and highly related individuals among communities point toward a panmictic genetic population with continuous gene flow among each of the communities. In species with slow life histories and fission-fusion dynamics, such as *Tursiops* spp., genetic and socio-spatial structures may reflect different timescales. Thus, despite genetic similarity, each social community should be considered as a distinct ecological unit to be conserved because they are exposed to different anthropogenic threats and occur in different ecological habitats, social structure being as important as genetic information for immediate conservation management. The estuarine community, in particular, is highly vulnerable and appropriate conservation measures are needed in order to maintain its connectivity with the adjacent, semi-enclosed coastal communities.

**Keywords:** bottlenose dolphins, population structure, microsatellites, mtDNA, gene flow, conservation, management units, relatedness

## INTRODUCTION

Social structure can play a critical role in the conservation of wildlife as it underpins the demography and behavior of a population and influences processes such as habitat use and dietary specialization (Snijders et al., 2017; Louis et al., 2018). Complex social structure and localized specialization are expected to promote isolation, which may create conservation challenges for

communities (i.e., sets of individuals that are behaviorally discrete from neighboring communities and within which most individuals associate with other members of the community, Wells et al., 1987) or populations unable to adapt to rapid environmental changes, notably human impacts in urbanized areas (Barragan-Barrera et al., 2017). Reduced intra-group social cohesion, for instance, appeared to affect the recovery of small populations of killer whales (Parsons et al., 2009; Williams et al., 2009). On the other hand, long-term social affiliations may contribute to natal site fidelity, potentially resulting in reduced gene flow among social groups and thereby shaping genetic variability within and between populations (Krützen et al., 2004; Möller and Beheregaray, 2004; Litz et al., 2012; Pratt et al., 2018).

The low cost of locomotion, high dispersal capabilities and lack of geographic barriers in the marine environment were thought to promote high levels of gene flow, but many taxa reveal surprising structuring even at small spatial scales (e.g., Palumbi, 1992; Taylor and Hellberg, 2003; Sellas et al., 2005). Genetic differentiation among communities and populations can result from recent divergence with no ongoing gene flow or long-term separation with low recurrent gene flow (Nielsen and Wakeley, 2001; Palsbøll et al., 2004). Discriminating between these scenarios has important implications for conservation, as isolated communities or populations may require management measures that are dependent upon their demographic patterns, ecological and social organization, as well as their levels of exposure to anthropogenic stressors (Yannic et al., 2016; Crawford et al., 2018).

Population genetic data have been increasingly used to delineate populations or communities of cetaceans into separate management units for the purposes of meeting conservation objectives (Taylor and Dizon, 1999; Palsbøll et al., 2007). Many of the coastal cetaceans lend themselves to such analyses as they tend to occur as genetically discrete population units, with differentiation being detected at small spatial scales relative to the distances over which they are capable of dispersing (e.g., spinner dolphins *Stenella longirostris*, Andrews et al., 2010; common dolphins *Delphinus delphis*, Möller et al., 2011; Bilgmann et al., 2014; Australian snubfin *Orcaella heinssohni* and humpback dolphins *Sousa sahulensis*, Brown et al., 2014; bottlenose dolphins *Tursiops* spp., Hoelzel et al., 1998b; Krützen et al., 2004; Fernández et al., 2011; Ansmann et al., 2012). Population differentiation of these species has been associated with habitat complexity, i.e., estuaries or bays versus open coastline (e.g., Möller et al., 2007), as well as resource or habitat specializations (e.g., Krützen et al., 2014; Louis et al., 2014; Giménez et al., 2018). While geographic isolation-by-distance results in differences between populations (e.g., Allen et al., 2016; Parra et al., 2018), genetic differentiation on particularly small spatial scales has also been attributed to factors pertaining to behavioral variation, including social structure and local philopatry (e.g., Wiszniewski et al., 2009; Andrews et al., 2010; Kopps et al., 2014; Van Cise et al., 2017).

Genetic structure in dolphins of the genus *Tursiops* is often highly habitat dependent. While there is relatively little differentiation for both nuclear and mitochondrial DNA markers in pelagic bottlenose dolphin populations (e.g., Hoelzel et al., 1998b; Quérrouil et al., 2007; Louis et al., 2014), stronger

differentiation on markedly smaller spatial scales has been described in coastal populations (Krützen et al., 2004; Sellas et al., 2005; Möller et al., 2007; Rosel et al., 2009; Tezanos-Pinto et al., 2009; Urian et al., 2009; Mirimin et al., 2011). Variation in oceanographic conditions such as salinity and temperature gradients, habitat type, as well as differences in prey preference and foraging specializations, have also been invoked to explain such fine-scale genetic differentiation (Natoli et al., 2005; Kopps et al., 2014; Krützen et al., 2014; Gaspari et al., 2015).

In the Perth metropolitan area, Western Australia, Indo-Pacific bottlenose dolphins (*Tursiops aduncus*, “bottlenose dolphins” hereafter) inhabit coastal, embayment and estuarine waters (Chabanne et al., 2017a). The population is exposed to year-round anthropogenic activities, including dredging, pile-driving, recreational and commercial shipping and fisheries, and environmental contaminants (Donaldson et al., 2010; Salgado Kent et al., 2012; Paiva et al., 2015; Cannell et al., 2016; Marley et al., 2017). Previous behavioral research recognized four well-defined communities with limited interactions, identified as Gage Roads (GR), Swan Canning Riverpark (SCR), Owen Anchorage (OA), and Cockburn Sound (CS) (Chabanne et al., 2017a,b). Three of these communities form relatively stable, cohesive units with long term residency in the area, occupying coastal embayment and estuarine habitats. The fourth community occurs along open coastline and appears structurally different, being much less socially cohesive and appearing to consist of more transient individuals (Chabanne et al., 2012, 2017a).

We investigated the extent of genetic structure and the degree of gene flow occurring among the four communities in Perth metropolitan waters using several genetic marker systems. We considered the well-documented social and spatial segregation of the four behaviorally defined communities when formulating conservation measures.

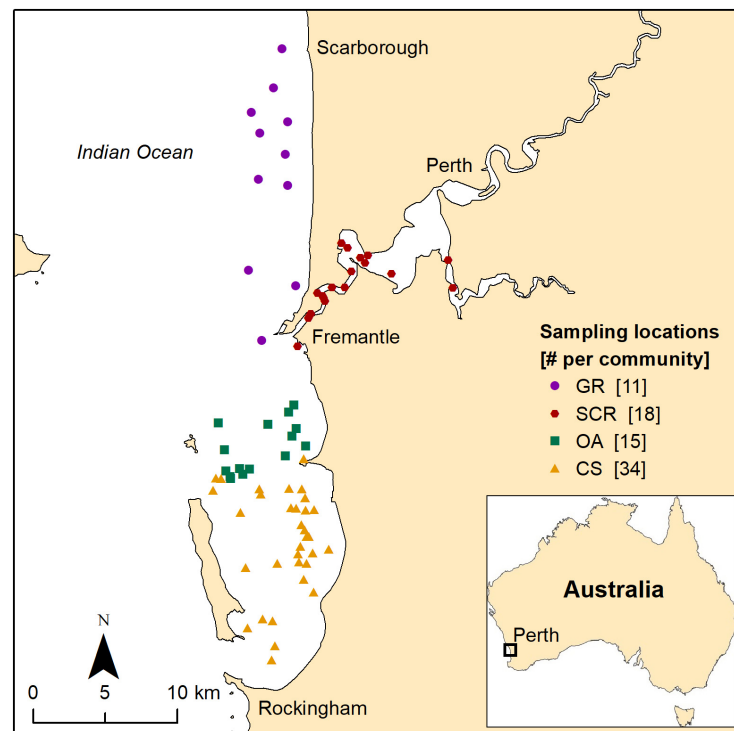
## MATERIALS AND METHODS

### Genetic Sample Collection

During systematic (Chabanne et al., 2017a) and opportunistic photo-identification surveys, we collected biopsy samples from Indo-Pacific bottlenose dolphins (*T. aduncus*) in Perth metropolitan waters, Western Australia (Figure 1), between 2007 and 2015 using a PAXARMS remote biopsy system (Krützen et al., 2002). Calves less than 2 years old (based on body length and approximate date of birth) were not sampled. Tissue samples were preserved in saturated NaCl 20% dimethyl sulfoxide (Amos and Hoelzel, 1991) until DNA extraction.

### DNA Extraction and Sexing

We extracted genomic DNA from skin samples using the Gentra Puregene Tissue Kit (Qiagen), following the manufacturer's protocol. We determined the sex of sampled individuals by amplifying parts of the ZFX and SRY genes (Gilson et al., 1998) via polymerase chain reaction (PCR) with 20–25 ng DNA, 0.15 µl of each primer (ZFX forward and reverse and SRY forward and reverse) and standard PCR reagents. The PCR profile consisted of initial denaturation at 95°C for 4 min, followed by 35 cycles of



**FIGURE 1** | Location of the sampled individuals of bottlenose dolphins associated with one of the four socio-spatial communities in Perth metropolitan waters, Western Australia. GR, Gage Roads; SCR, Swan Canning Riverpark; OA, Owen Anchorage; CS, Cockburn Sound.

94°C for 45 s, 50°C for 45 s, and 72°C for 10 min (Natoli et al., 2004; Ansmann et al., 2012). PCR products were separated on agarose gel to determine sex base on length differences.

## Genotyping and Validation of Microsatellites

We successfully genotyped 87 non-duplicated samples for 32 microsatellite loci: D1rFCB4, D1rFCB5 (Buchanan et al., 1996), LobsDi\_7.1, LobsDi\_9, LobsDi\_19, LobsDi\_21, LobsDi\_24, LobsDi\_39 (Cassens et al., 2005), SCA9, SCA22, SCA27 (Chen and Yang, 2008), TexVet5, TexVet7 (Rooney et al., 1999), KWM12 (Hoelzel et al., 1998a), EV37 (Valsecchi and Amos, 1996), MK3, MK5, MK6, MK8, MK9 (Krützen et al., 2001), Tur\_E12, Tur4\_66, Tur4\_80, Tur4\_98, Tur4\_105, Tur4\_108, Tur4\_111, Tur4\_117, Tur4\_128, Tur4\_132, Tur4\_142, Tur4\_153, and Tur4\_162 (Nater et al., 2009). We amplified the loci following the PCR method described in Frère et al. (2010) and in Marfurt (2019). Single stranded PCR products were run on an ABI 3730 DNA Sequencer (Applied Biosystems). We scored microsatellite alleles using GENEIOUS 9.1<sup>1</sup> (Kearse et al., 2012) with the microsatellite plugin 1.4 (Applied Biosystems). Our genotyping error rate based on 11 individuals scored twice was estimated to be 0.27%, i.e., one incorrect genotype out of 360 scored. Although dolphin calves were not sampled, our study was sufficiently long for some individuals to be sampled when older. All scored individuals were cross-checked for eventual

duplicates not initially identified (i.e., misidentification due to change of the dorsal fin). To minimize biases associated with first-order (parent–offspring, full-siblings) related individuals when assessing genetic structure, we removed any known offspring and juveniles from our dataset ( $n = 9$  individuals). Later, we also calculated the relatedness between all possible dyads using the R package “related” (Pew et al., 2014) using the TrioML estimator and tested differences within and between communities using a Mantel test and  $10^4$  permutations.

After checking for null alleles and scoring errors due to stuttering or large allele dropout using the software Micro-Checker 2.2.3 (Van Oosterhout et al., 2004), we removed four microsatellite loci (SCA27, TexVet5, MK8, and Tur4\_80). No deviation from Hardy-Weinberg equilibrium (HWE) and no evidence of linkage disequilibrium (LD) were detected between the remaining loci and across communities using the Markov chain randomization in the package “genepop” (Rousset, 2008, 2020) with  $10^5$  dememorizations,  $10^3$  batches, and  $10^4$  iterations and the Bonferroni correction (Rice, 1989).

## Mitochondrial (mt) DNA Sequencing

We amplified a 412-bp mitochondrial fragment using the primers dlp1.5 (5′-TCA CCC AAA GCT GRA RTT CTA-3′) and dlp5 (5′-CCA TCG WGA TGT CTT ATT TAA GRG GAA-3′) (Baker et al., 1993) and following the PCR conditions described in Bacher et al. (2010). We successfully obtained mtDNA sequences for 73 out of the 78 samples used in the nuclear analyses after manually edited them in GENEIOUS 9.1.

<sup>1</sup><http://www.geneious.com>



## Genetic Diversity

We assessed the genetic diversity based on microsatellite alleles within each of the four communities by calculating the number of alleles ( $N_a$ ), effective number of alleles ( $N_e$ ), private alleles ( $N_{PA}$ ), observed ( $H_O$ ) and expected ( $H_E$ ) heterozygosities in GenAEx (Peakall and Smouse, 2012), and allelic richness ( $A_R$ ) using FSTAT 2.9.3 (Goudet, 2001). We estimated inbreeding coefficient ( $F_{IS}$ ) for each community separately and pooled as one population in Arlequin 3.5 (Excoffier and Lischer, 2010) testing for significance with  $10^4$  permutations. We also evaluated the possibility of inbreeding using INEST 2.2 (Inbreeding/Null Allele Estimation; Chybicki and Burczyk, 2009) and taking into account the estimated null allele frequencies considering null alleles (Chybicki, 2017). For mtDNA, we identified the number of haplotypes ( $NH$ ), and estimated haplotype ( $h$ ) and nucleotide ( $\pi$ ) divergence using DnaSP 5.10 (Librado and Rozas, 2009).

## Genetic Differentiation

We estimated pairwise genetic differentiation of microsatellite alleles ( $F_{ST}$ ) (Weir and Cockerham, 1984) and mtDNA  $\Phi_{ST}$  (Tamura and Nei, 1993) among communities using Arlequin 3.5 (Excoffier and Lischer, 2010). For mtDNA, the choice of the model used was made after computing several nucleotide substitution models in jModelTest 2.1 (Posada, 2008). Although the minimum corrected Akaike Information Criterion ( $AIC_c$  used for small sample size) suggested Hasegawa-Kishino-Yano (Hasegawa et al., 1985) as the best model, this one was unavailable in Arlequin, and therefore we used the Tamura-Nei model (TrN, Tamura and Nei, 1993) as the next best model ( $\Delta AIC_c < 2$ ). All pairwise comparisons were testing for significance with  $10^4$  permutations.

## Genetic Population Structure

Given the challenges associated with the inference of the most likely number of distinct genetic clusters ( $K$ ) in a population (Guillot et al., 2009), we assessed  $K$  in Perth metropolitan waters based on the microsatellite loci using four approaches to ensure the robustness of the results: (1) a Bayesian clustering algorithm implemented in STRUCTURE 2.3 (Pritchard et al., 2000), (2) a least-squares optimization approach taking into account spatial autocorrelation based on tessellation (Caye et al., 2016) with the R package “tess3r” (Caye et al., 2017), (3) a discriminant analysis of principal components (DAPC) that allows to maximize the differences between groups while minimizing variation within groups (Jombart et al., 2010) using the package “adegenet” (Jombart and Ahmed, 2011), and (4) a three-dimensional factorial correspondence analysis (FCA) that seeks to identify genetic affinities between individuals and alleles and performed in GENETIX (Belkhir et al., 2004).

In STRUCTURE, we conducted the analysis without and with LOCPRIOR models that assigned samples to their respective socio-spatial community, as defined in Chabanne et al. (2017a). Using a LOCPRIOR model improves clustering when the signal is weak without spuriously inferring structure (Hubisz et al., 2009). We performed the analysis using the admixture model with correlated allele frequencies (Falush et al., 2003), using

a burn-in of  $10^6$  Markov Chain Monte Carlo (MCMC) steps followed by  $10^7$  MCMC steps. We repeated each run 10 times for  $K$  varying from one to six ( $K = 5$  and  $6$  being used to enable calculation of  $\Delta K$ ). The most likely value of  $K$  was determined by averaging the log probability  $\ln P(D)$  among runs for each  $K$  value, and selecting the highest mean  $\ln P(D)$  (Pritchard et al., 2000). Individual genetic cluster assignment estimates (i.e., individual ancestry proportions) were generated for each set for  $K$  varying from two to four, using the web service software CLUMPAK (Kopelman et al., 2015). The TESS analysis included the GPS coordinates (latitude and longitude, WGS84) of the sampled individuals as *a priori* information (Durand et al., 2009). We replicated ten runs for each  $K$  value varying from two to six. The most likely number of genetic clusters was identified by plotting the scores of a cross-validation with the best  $K$  value corresponding to a plateau before generating a  $q$  matrix containing individual admixture coefficients (Frichot et al., 2015). We then performed the DAPC analysis following Jombart and Collins (2015) with the maximum number of clusters set to six. The most likely number of genetic clusters was identified by the lowest Bayesian Information Criterion (BIC) value. Finally, we also assessed the structure with an FCA without *a priori* community information. The 3D FCA representation was carried out using the R package “scatterplot3d” (Ligges et al., 2018).

## Assessment of Gene Flow

Using GENECLASS 2.0 (Piry et al., 2004), we looked for possible first-generation migrants (referred to as the likelihood of migrant detection  $L$ ) among the communities following the Bayesian computation criteria of Rannala and Mountain (1997). This analysis was based on the likelihood of an individual's genotype arising from the communities where the individual was sampled given the observed set of allele frequency ( $L_{HOME}$ ) and the highest likelihood value among all potential source communities ( $L_{MAX}$ ), including the home community where the individual was sampled, such as  $L = L_{HOME}/L_{MAX}$ . Significance of the assignment of individuals was assessed with MCMC resampling of  $10^4$  individuals and a threshold of 0.05 (Paetkau, 2004). This analysis was repeated using  $L = L_{HOME}$  as the likelihood computation to account for the uncertainty that all source populations were sampled (Piry et al., 2004). We then estimated the effective numbers of migrants per generation between communities based on the Mutual information ( $S_{H_{ua}}$ ) calculated in GenAEx 6.5 (Peakall and Smouse, 2012). We also used equations 10b and 10c (Sherwin et al., 2006), allowing us to estimate the effective number of individuals exchanged per generation ( $N_{em}$ ) with and without  $N_e$  known, respectively. Given the small population size here, we estimated  $N_e$  as the sum of the samples available for the communities for which the migration rate was calculated.

## RESULTS

### Genetic Diversity

Autosomal levels of genetic diversity were significantly higher in CS than in other communities, with more than two thirds of

**TABLE 1** | Genetic diversity measures (SE) for bottlenose dolphin socio-spatial communities using microsatellite loci ( $n = 28$ ) and mtDNA.

	Microsatellites										mtDNA			
	<i>N</i>	<i>Nf</i>	<i>Nm</i>	<i>N<sub>A</sub></i>	<i>N<sub>e</sub></i>	<i>N<sub>PA</sub></i>	<i>A<sub>R</sub></i>	<i>H<sub>E</sub></i>	<i>H<sub>O</sub></i>	<i>F<sub>IS</sub> (FSTAT) (INEST)</i>	<i>n</i>	<i>NH</i>	<i>h</i>	$\pi$
Overall	78	38	40	4.955 (0.247)	3.119 (0.149)	—	4.422 (0.362)	0.589 (0.020)	0.621 (0.022)	−0.020 <sup>NS</sup> 0.008 <sup>\$</sup>	73	5	0.581 (0.047)	0.013 (0.002)
GR	11	4	7	4.607 (0.458)	3.122 (0.330)	2	4.401 (0.427)	0.572 (0.043)	0.603 (0.049)	−0.006 <sup>NS</sup> 0.012	8	4	0.750 (0.139)	0.020 (0.007)
SCR	18	10	8	4.643 (0.466)	3.045 (0.302)	6	4.111 (0.369)	0.581 (0.040)	0.596 (0.042)	0.006 <sup>NS</sup> 0.026 <sup>\$</sup>	16	3	0.425 (0.133)	0.018 (0.005)
OA	15	8	7	4.679 (0.418)	2.965 (0.253)	1	4.139 (0.326)	0.590 (0.035)	0.627 (0.041)	−0.029 <sup>NS</sup> 0.006	15	3	0.629 (0.086)	0.022 (0.004)
CS	34	16	18	5.893 (0.601)	3.346 (0.316)	23	4.415 (0.396)	0.611 (0.041)	0.656 (0.045)	−0.059 <sup>**</sup> 0.004	34	3	0.533 (0.042)	0.004 (0.002)

*n*, number of samples; *Nf*, number of females; *Nm*, number of males; *N<sub>A</sub>*, mean number of alleles; *N<sub>e</sub>*, mean effective number of allele; *N<sub>PA</sub>*, number of private alleles; *A<sub>R</sub>*, mean allelic richness; *H<sub>E</sub>*, expected heterozygosity; *H<sub>O</sub>*, observed heterozygosity; *F<sub>IS</sub>*, Inbreeding coefficient (NS, Non-Significant  $P > 0.05$ ); *NH*, number of haplotypes; *h*, Haplotype diversity;  $\pi$ , nucleotide diversity. GR, Gage Roads; SCR, Swan Canning Riverpark; OA, Owen Anchorage; CS, Cockburn Sound. Inbreeding significant smaller than observed <sup>\*\*</sup> $P$ -value  $< 0.01$  (Bonferroni correction), <sup>NS</sup>Non-significant, <sup>\$</sup>important component based on INEST best model.

**TABLE 2** | Pairwise comparison between the four socio-spatial communities for 28 microsatellite loci ( $F_{ST}$ , above diagonal) and for mtDNA ( $\Phi_{ST}$ , below diagonal).

Community	GR	SCR	OA	CS
GR	—	0.007	0.010	0.021 <sup>**</sup>
SCR	0.000	—	0.021 <sup>*</sup>	0.018 <sup>***</sup>
OA	0.000	0.000	—	0.019 <sup>**</sup>
CS	0.168	0.190	0.280 <sup>*</sup>	—

GR, Gage Roads; SCR, Swan Canning Riverpark; OA, Owen Anchorage; CS, Cockburn Sound.  $P$ -value <sup>\*</sup> $< 0.05$ ; <sup>\*\*</sup> $< 0.01$ ; <sup>\*\*\*</sup> $< 0.001$  after sequential Bonferroni correction.

the private alleles identified in CS (Table 1). Other communities showed similar genetic diversity (Table 1). For mitochondrial DNA, we found a total of 20 polymorphic sites, defining five haplotypes (Table 1). In contrast to autosomal data, haplotype diversities were significantly lower in CS and SCR.

## Genetic Differentiation

For autosomal markers, the CS community showed small albeit significant levels of differentiation from all other communities, which was also the case for SCR and OA (Table 2). To verify the accuracy of the significant values of  $F_{ST}$  reported here, the simulation run in POWSIM indicated that we would be able to detect an  $F_{ST}$  of 0.018 and above with 100% confidence, 0.010 with 99.40% confidence, and 0.007 with 93.90% confidence, while the type I error probability was lower than the expected rate of 5%. For mtDNA ( $\Phi_{ST}$ ), significant differentiation was found between OA and CS only (Table 2).

## Genetic Structure

Based on the highest mean of the estimated posterior probabilities [ $\ln P(D)$ ], the STRUCTURE analyses suggested  $K = 2$  to be the most likely number of genetic clusters, while DAPC analysis suggested no clustering (Supplementary

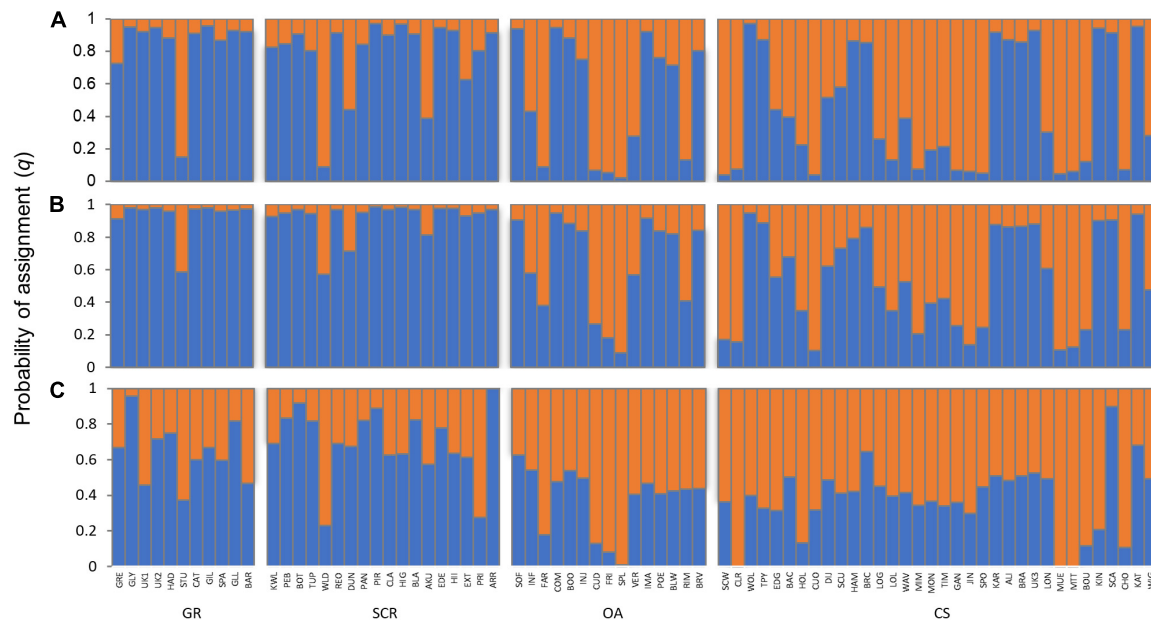
Figure 1). The cross-validation from the TESS method did not exhibit a minimum value or a clear plateau to identify the most likely number of genetic clusters  $K$  (Supplementary Figure 1). Both the OA and CS communities appeared to contain individuals belonging to one of the identified clusters or were admixed (Figure 2). Clustering assignment for individuals from GR and SCR contrasted between the results from STRUCTURE and TESS, with the former suggesting that the majority of the individuals were assigned to the same cluster (minimum of 82% and 78% with  $q > 0.8$  in GR and SCR, respectively), while the latter indicated many individuals to be admixed (Figure 2).

The 3D FCA showed no clustering (factors 1–3 explaining only 13.98% of the variation, Figure 3) and samples were generally scattered.

The median-joining network using mtDNA revealed no clear clustering based on socio-spatial communities with most of the haplotypes being shared between communities, despite showing two main ancestral groups of haplotypes separated by at least 15 mutational steps (Figure 4). However, most samples were represented in one matriline group with haplotype H3 found in the majority of the samples (57, 75, 53, and 50% for GR, SCR, OA, and CS, respectively). The low level of nucleotide diversity found in CS (0.004 and Table 1) is consistent with all but one sample (WOL with H1) having haplotypes from the same ancestral matriline group (H2 and H3, Figure 4) and separated by a maximum number of mutations ( $n = 17$ ).

## Contemporary Dispersal

The assignment/exclusion test in GENECLASS2 indicated that only 59% of the individuals were correctly assigned to their respective socio-spatial communities and detected 17 first-generation migrants in all directions, except from CS to SCR (Supplementary Table 1). Based on the estimated mutual information ( $^S H_{ua}$ , Supplementary Table 2), we estimated the effective number of individuals exchanged per generation ( $N_{em}$ )



**FIGURE 2 |** Assignment probabilities of individual bottlenose dolphins based on 28 microsatellite loci and inferred for  $K = 2$  using methods implemented in STRUCTURE **(A)** without LOCPRIOR, **(B)** with LOCPRIOR, and **(C)** in TESS. Each vertical line represents one individual, with the colors indicating the membership proportions ( $q$ ) to each of the genetic clusters. Individuals are grouped by socio-spatial communities (GR, Gage Roads; SCR, Swan Canning Riverpark; OA, Owen Anchorage; CS, Cockburn Sound).

varying from 2.33 to 4.97 and from 4.90 to 8.69 when  $N_e$  was estimated based on the number of samples available for each community pair (Table 3).

## Relatedness

Comparison of intra- and inter-community relatedness indicated significantly higher values within communities than between communities (Mantel test,  $r = 0.1327$ , and  $P$ -value  $< 0.001$ ). Notably, individuals related at the first-order level (parent-offspring, full-siblings; for the purpose of this study defined by having a pairwise relatedness value of 0.3811 or larger, the lowest value observed from a known mother-calf pair in this study) were found primarily within communities rather than between (Figure 5). Half-siblings ( $r > 0.25$ ) were roughly equally represented within and between communities with 4.6 and 2.4% of the pairs, respectively (Figure 5). Removing at least one individual from each first-order pair had no bearing on genetic differentiation and genetic structure analyses (Supplementary Table 3).

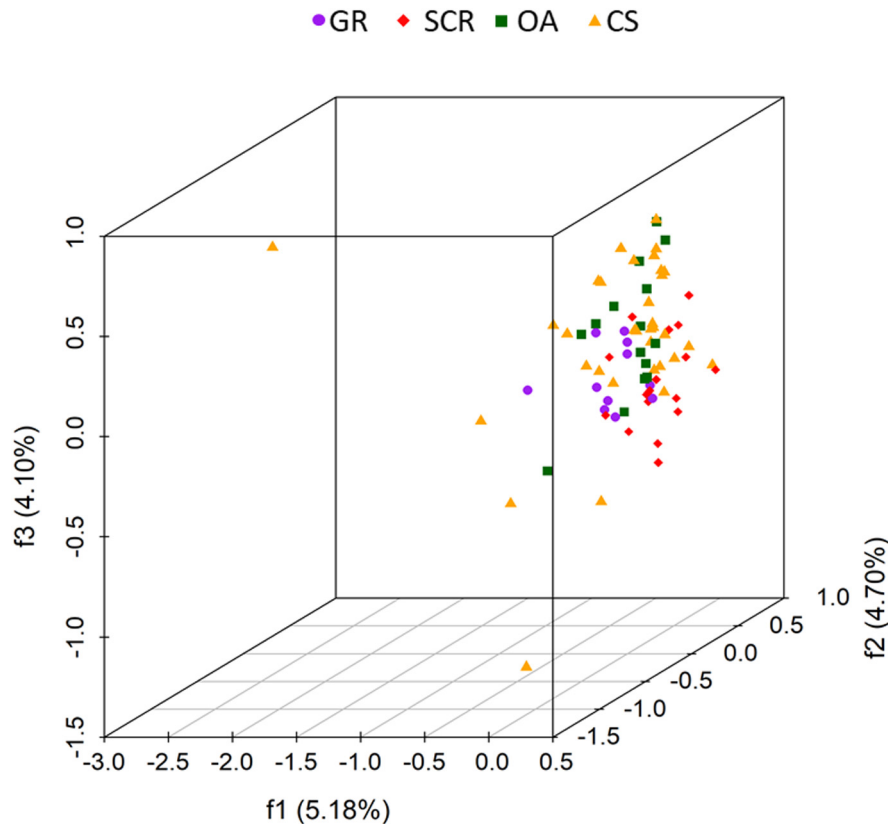
## DISCUSSION

Overall, we found evidence for one panmictic bottlenose dolphin population with continuous gene flow. Analyses of both microsatellites and mtDNA markers revealed no conclusive structure, despite using various clustering algorithms that can produce different solutions due to differences in the underlying models and prior assumptions (Francois and Durand, 2010), and only low nuclear differentiation ( $F_{ST} < 0.021$ ) among the four

socio-spatial communities. This may be due to the presence of highly related individuals in our data, mirroring family structures present within each community (Latch et al., 2006; Anderson and Dunham, 2008; Pritchard et al., 2010). The *post hoc* removal of highly related individuals leading to even lower levels of differentiation (results in Supplementary Table 3) supports this hypothesis.

The disconnect between genetic and behavioral structures is to some extent unexpected. Other studies comparing communities of *T. aduncus* (e.g., Möller et al., 2007; Wiszniewski et al., 2010) and its congener *T. truncatus* (e.g., Mirimin et al., 2011; De Los Angeles Bayas-Rea et al., 2018) detected fine-scale genetic structure at a similar geographic scale. The presence of genetic structure may indicate limited gene flow between communities, perhaps due to behavioral specializations or environmental discontinuities (Wiszniewski et al., 2010). The permanent dispersal described here, with the detection of first-generation migrants and high migration rates among communities, could reduce inbreeding within communities (Mills and Allendorf, 1996; Perrin and Mazalov, 1999; Faubet et al., 2007).

The low travel costs associated with short distances between the communities in Perth metropolitan waters provide the potential for reproduction outside social groups (Connor, 2000) without the necessity for individuals to permanently leave them. Killer whales, for example, live in permanent social groups from which males temporarily emigrate to mate with females from other groups (Pilot et al., 2010; Martien et al., 2019). In our study, some SCR resident males were observed herding reproductive females from OA into SCR (data not published), with females returning to their community core



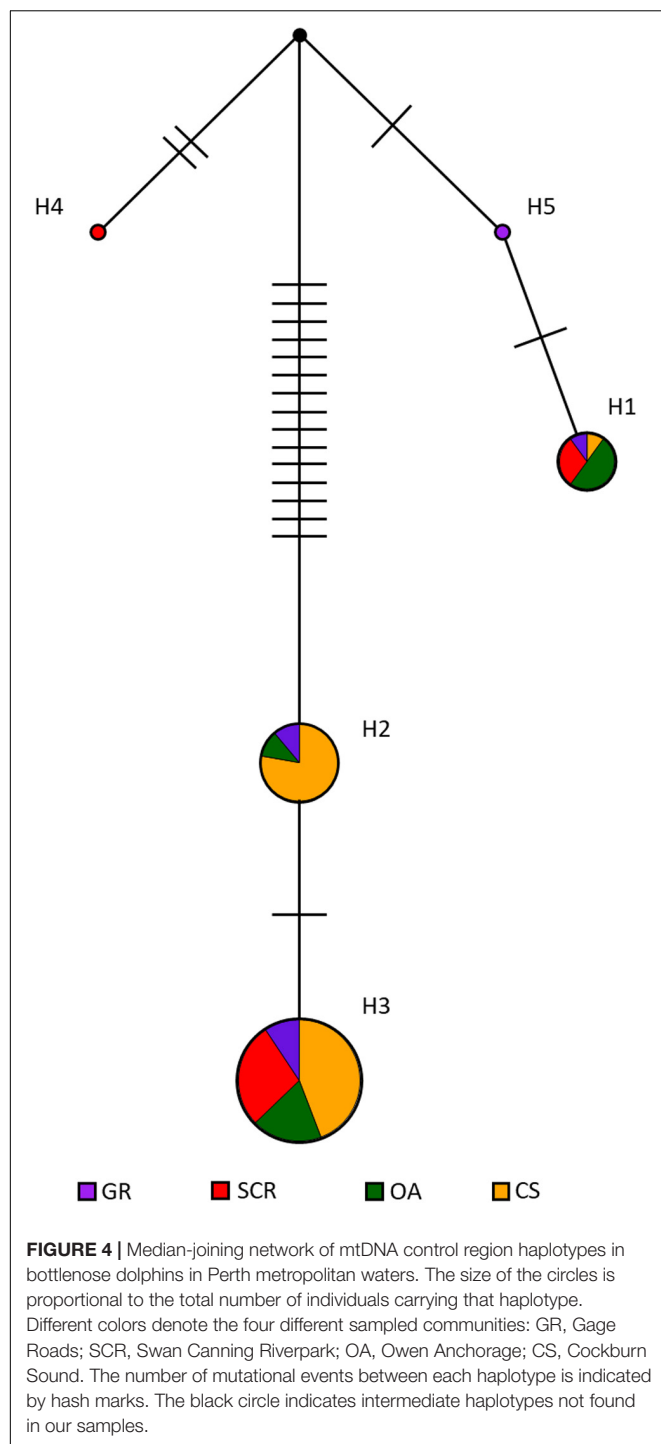
**FIGURE 3 |** Factorial correspondence analysis (FCA) three-dimensional plots of microsatellite variation of bottlenose dolphins based on 28 microsatellite loci and without *a priori* information on socio-spatial communities. Each dot represents one individual, with the color/shape indicating its designated socio-spatial community (GR, Gage Roads; SCR, Swan Canning Riverpark; OA, Owen Anchorage; CS, Cockburn Sound). The percentage of variation explained by each of the first three factors are given in parentheses.

area afterward, a behavior recorded elsewhere for this species (Tsai and Mann, 2013; Wallen et al., 2016) and supported by the presence of a few highly related pairs of individuals from different communities.

Theory suggests that animals forming social groups may favor close relatives (Hamilton, 1964a,b). This appears to occur among dolphins of Perth metropolitan waters, as we found relatedness levels to be significantly higher within than between communities. Additionally, we found highly related individuals that were members of different communities. Such relatedness structure appears to be reflected by the long lifespan and slow life history leading to highly overlapping generations in bottlenose dolphins (Wells and Scott, 2002), as well as fission-fusion dynamics (Connor et al., 2000). Indeed, the maximum estimate of residency time (i.e., site fidelity) was 18 years (Chabanne et al., 2017a), a period considerably less than maximum life span in this species (i.e., more than 40 years; Wang and Yang, 2009). Individuals may switch communities in response to significant events (e.g., loss of a social partner, a new resource becoming available). Thus, the lack of genetic structure among social communities may mirror past and present fission-fusion dynamics among the communities as they overlap on the edge of their home range.

While genetic parameters do not match socio-spatial structure in this study, other factors need to be considered for management purposes. Over the last two decades, anthropogenic impacts were variable between communities (Chabanne et al., 2017a). Differences in habitat quality and population density commonly influence dispersal between populations, with areas characterized by lower-quality habitat and lower-density requiring an influx of dispersing individuals from higher-quality and higher-density areas for populations to persist (Pulliam, 1988; Figueira and Crowder, 2006; Liggins et al., 2013; Draheim et al., 2016; Sundqvist et al., 2016). Within Perth metropolitan waters, environmental changes associated with anthropogenic activities varied among the sites, requiring site-specific management strategies. Indeed, a gradual decline of seagrass and fish communities have been observed for the last three decades in SCR, in addition to problems common in other urban estuaries, such as eutrophication, deoxygenation, algal blooms, and the presence of per- and polyfluorinated alkyl substances (PFAS), a group of synthetic industrial chemicals (Deeley and Paling, 1998; Nice, 2009; Kilminster and Forbes, 2014; Valesini et al., 2017). In CS, important loss of seagrass coverage occurred between the 1960s and 1990s, with no substantial recovery of seagrasses on the eastern shelf (Kendrick et al., 2002) as a result of remaining





problems associated with nutrient influx from groundwater plumes and contaminated sediments (Fraser and Kendrick, 2017). Also, changes in fish diversity were found along a gradient north to south (Sampey et al., 2011), indicating variation in suitable fish habitat that could result in heterogeneous dolphin distribution. In comparison, seagrass coverage in OA has not changed or even increased (Kendrick et al., 2000) despite dredging occurring year-round since 1972, suggesting a better

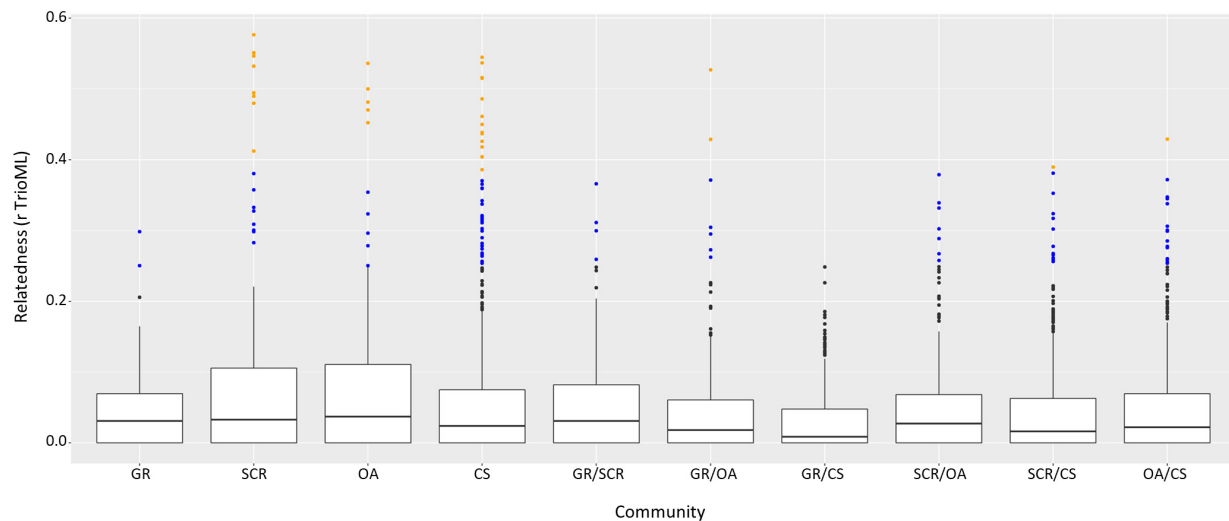
**TABLE 3 |** Effective number of individuals exchanged per generation ( $N_{em}$ ) between communities estimated without knowledge of  $N_e$  [equation 10c from Sherwin et al. (2006), estimates below the diagonal] and with our estimate of  $N_e$  as the sum of the paired communities [equation 10b from Sherwin et al. (2006), estimates above the diagonal with  $N_e$  between brackets].

Community	GR	SCR	OA	CS
GR	–	5.36 (29)	4.90 (26)	8.31 (45)
SCR	2.88	–	5.37 (33)	8.69 (52)
OA	2.91	2.33	–	7.38 (49)
CS	3.45	3.04	4.97	–

GR, Gage Roads; SCR, Swan Canning Riverpark; OA, Owen Anchorage; CS, Cockburn Sound.

habitat supporting a broad assemblage of prey species for dolphins. Ongoing, past and future environmental impacts (i.e., development of an Outer Harbor in CS) described above suggest that habitat and oceanographic characteristics, physical barriers, and dietary specializations are all conditions that may lead to discontinuous ecological communities, potentially representing unique ecological units to conserve even in the absence of genetic structure (Giménez et al., 2018). In this context, future research may disentangle the socio-spatial structure of bottlenose dolphins in Perth metropolitan waters.

Finally, none of these communities are safe from reductions in genetic diversity should stochastic events lead to a bottleneck (Storz, 1999; Leffler et al., 2012; Vachon et al., 2018). The low haplotype diversity found in CS could be suggestive of the occurrence of an historical bottleneck event or selection (Rand, 1996). Such scenarios are often challenging to evaluate because of the difficulty in assessing small sample sizes or when there is low effective population size pre-bottleneck (Bjorklund, 2003; Peery et al., 2012; Subramanian, 2016). The SCR lost almost 1/3 of its individuals (Chabanne et al., 2012) in 2009 from an outbreak of the cetacean morbillivirus (CeMV), which has also affected several other dolphin populations worldwide (Holyoake et al., 2010; Stone et al., 2011; West et al., 2012; Casalone et al., 2014; Stephens et al., 2014; Kemper et al., 2016). After the event, there was a noteworthy decrease in mtDNA haplotypes from at least seven before 2010 (Holyoake et al., 2010) to only three in the SCR (this study), with a potential loss of haplotypes at Perth population scale, i.e., only five defined in this study, while Manlik et al. (2019) described 10 haplotypes using a subsample of the Perth population. Mortalities caused by viral pandemics, environmental pollution or human activities have already negatively affected population size and genetic diversity in other species of dolphin (Pichler and Baker, 2000; Krützen et al., 2018). Although more work is required to better understand possible selection processes associated with resistance to CeMV (Batley et al., 2019), the reduction in genetic diversity exacerbated by the negative effects of genetic drift in small populations and potential inbreeding, and thus lower resilience to stochastic processes, poses an extinction risk to some cetacean populations (Oremus et al., 2015).



**FIGURE 5 |** Pairwise relatedness among and between communities using the triadic likelihood (TrioML) estimator. Outliers in orange represent first-order pairwise defined with  $r > 0.3811$  (percentage of those pairs respective to the number of pairs available are noted above the figure). Outliers in blue represent half-sibling order pairwise ( $r > 0.25$ ).

## CONCLUSION

Our study suggests that the present socio-spatial structure of Indo-Pacific bottlenose dolphins in Perth metropolitan waters does not reflect a genetic structure defined by a clear separation between communities. Managers might then consider that, should any of these communities (CS, GR, SCR, and/or OA) become extinct, the locality of the community would be repopulated by members of one or more of the adjacent communities. However, the recovery of dolphin abundance to original numbers or the re-colonization of available habitats is likely to be hampered if the cause of the community decline and local extinction in the first place is not correctly identified and managed accordingly (Irwin and Würsig, 2004; Nichols et al., 2007). Therefore, each community should still be considered a distinct ecological unit to conserve based on the available information on anthropogenic stressors and that presented here, as well as in Chabanne et al. (2017a).

The lack of fine-scale genetic structure should not lead to the conclusion that no population structure exists [e.g., Louis et al. (2018) and Giménez et al. (2018)]. The discrete social and spatial parameters, the long-term residency of the communities and the higher relatedness found within than between communities still support community-specific management actions (Chabanne et al., 2017a). Other extrinsic factors such as resource availability, habitat, or foraging specializations have significant explanatory power of socio-spatial structure in dolphin populations (Krützen et al., 2004; Möller et al., 2007; Ansmann et al., 2012; Kopps et al., 2014; Giménez et al., 2018; Louis et al., 2018). Any ecological differences between communities must therefore be considered and, in some circumstances, may be as informative as genetic differences (Taylor, 2005; Giménez et al., 2018; Louis et al., 2018). Until further research can be done to better understand the consequences of high

intra-community relatedness, and despite the communities appearing to belong to a single panmictic population, the different anthropogenic threats support the current socio-spatial division for practical conservation management. With increased environmental stochasticity, even comparatively large dolphin populations have been subject to significant negative impacts on demographic and vital rates (e.g., Wild et al., 2019). In particular, the estuarine SCR community in Perth waters appears highly vulnerable to rapid environmental change and appropriate conservation measures are needed, in addition to maintaining connectivity between it and the coastal communities.

## DATA AVAILABILITY STATEMENT

Microsatellite genotypes are available in the figshare repository, doi: 10.6084/m9.figshare.13078823. Haplotype sequences were deposited into GenBank under Accession numbers MW221830 to MW221834.

## ETHICS STATEMENT

The animal study was reviewed and approved by the Animal Ethics Committee, Murdoch University.

## AUTHOR CONTRIBUTIONS

DC conceived and designed the study and processed the data. DC and SA collected the data. DC analyzed the data with advice

from MK and WS. DC wrote the manuscript, with contributions to drafting, review and editorial input from MK, SA, HF, and WS. All authors contributed to the article and approved the submitted version.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2020.617540/full#supplementary-material>

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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